# Visual perception: **Monkeys see things our way**

Charles E. Connor

**Neural mechanisms of visual perception can be studied in detail only in non-human animals. But recent work in humans has revealed a striking functional homology between the human and monkey visual systems, confirming the relevance of animal data and establishing a paradigm for cross-species studies of brain function.**

Address: Johns Hopkins University, 338 Krieger Hall, 3400 North Charles Street, Baltimore, Maryland 21218, USA.
E-mail: connor@jhu.edu

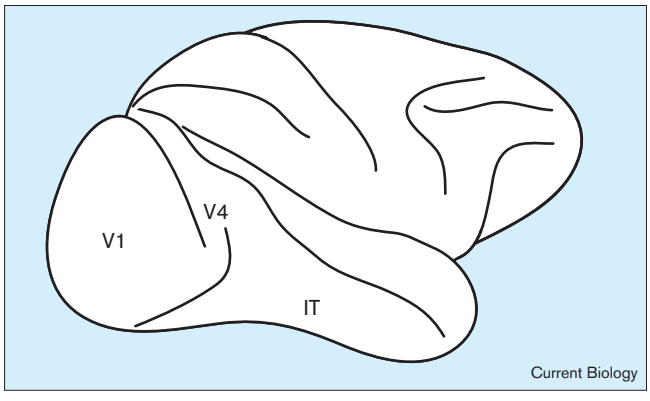
**Current Biology** 2000, 10:R836–R838

0960-9822/00/$ – see front matter


Our understanding of human brain function depends on the application of an array of complementary experimental methods. Psychological studies elucidate *what* the brain can do, by measuring the perceptual and cognitive capacities of human subjects. Functional brain imaging, electroencephalography and the study of patients with brain injuries reveal *where* in the brain — and to some extent *when* or in what sequence — various functions are carried out. The question of *how* particular brain regions really operate, at the level of detailed neural mechanisms, can be addressed empirically only by neurophysiological and neuroanatomical experiments in non-human animals.

The past few years have seen increasing convergence between human and animal studies of brain function.

**Figure 1**




Lateral view of a macaque monkey right hemisphere. Areas V1, V4 and IT represent early, intermediate and late stages, respectively, in the ventral, object-related pathway of visual processing. (The location of V4v in the human brain is shown in Figure1 of the Wilkinson *et al.* [2] paper, elsewhere in this issue.)

Imaging and brain-injury patient studies have established functional homologies between brain regions in humans and monkeys. This greatly enhances the relevance of neurophysiological and neuroanatomical studies in animals for understanding human brain function. Two recent articles about visual area V4, one by Gallant *et al.* [1] and the other, in this issue of *Current Biology*, by Wilkinson *et al.* [2], illustrate this kind of convergence. By linking human V4 function with the extensive data available on monkey V4, these studies help to illuminate the neural basis of our ability to perceive and recognize visual objects.

Visual area V4 was originally described in monkeys. It is an intermediate stage in the ventral visual pathway of the primate brain (Figure 1). The ventral pathway is thought to process information about objects, in contrast to the dorsal pathway, which is thought to process information about spatial location and movement [3]. Both the ventral and dorsal pathways originate in primary visual cortex, V1, where individual neurons function somewhat like pixels in a television image, each representing properties such as color or edge orientation within a small image region. The ventral pathway terminates in the ventral or inferior portion of the temporal lobe, known as inferotemporal (IT) cortex, a complex of visual regions in which some neurons appear to encode abstract object categories such as faces and hands. Area V4 is immediately antecedent to IT cortex.

Neural operations in area V4 are bound to be a key stage in the transformation from the pixel-like representation in V1 to the abstract representation in IT cortex. Early neurophysiological experiments in monkeys showed that V4 neurons are highly sensitive to color [4], and previous studies of human V4 have largely focused on color perception. More recent neurophysiological and lesion experiments in monkeys have shown that area V4 processes intermediate-level shape information, such as curvature, and is intimately involved in attentional processes. Both of these properties relate to area V4's transformational role in object recognition.

According to most theories, object recognition depends on the identification of object parts and elucidation of their spatial relationships. Cells in area V4 appear to represent intermediate features, such as angles and curves, that make up more complex shapes [5,6]; they may also encode the spatial relationships between those features [7]. Object recognition also depends critically on selective attention, because a typical visual scene contains too many objects to process simultaneously. V4 cells are strongly modulated by selective attention, responding best to

attended objects and filtering out unattended stimuli [8]. It is the role of V4 in intermediate shape processing and attentional phenomena that Gallant *et al.* [1] and Wilkinson *et al.* [2] have explored in humans.

Gallant *et al.* [1] studied a patient, AR, with a small lesion at the site of ventral human V4 (V4v). The position of human V4v has been established by mapping the various topographic representations of visual space in human cortex using functional magnetic resonance imaging (fMRI) [9,10]. There is not complete consensus in the field on this, however — a dissenting view is that area V4 corresponds to a more anterior, highly color-sensitive region [11], which one group has labeled V8 [12]. AR's right hemisphere V4v lesion, revealed by anatomical MRI, affects perception in the upper left quadrant of visual space. Initial neurological testing of AR disclosed a deficit in color perception, known as achromatopsia, in this quadrant.

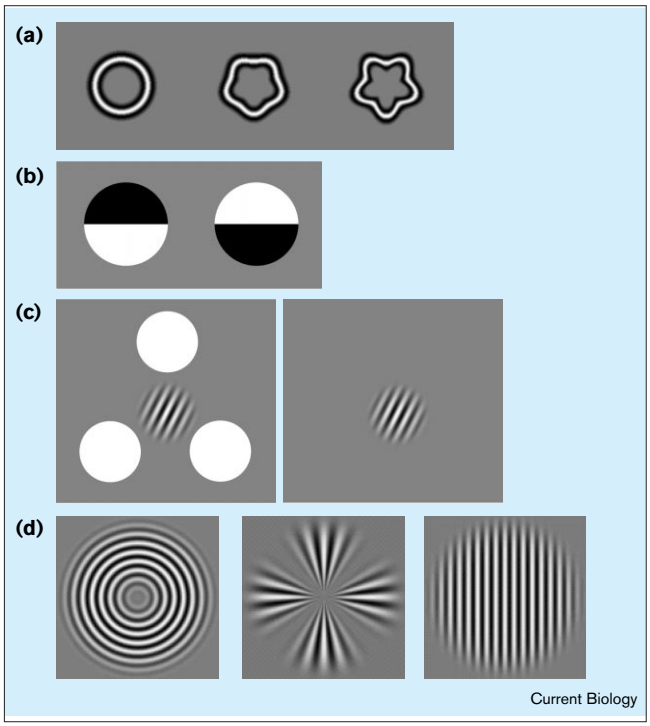
Gallant *et al.* [1] developed a battery of tests that were designed to invoke V4-level shape or attention processing, based on previously published monkey neurophysiology and lesion studies. As neurophysiological studies have shown that V4 cells are sensitive to curvature [5,6], several of the tests involved curvature perception. Example stimuli from one of these tests are shown in Figure 2a. The patient was required to fixate his gaze on a small target on a computer screen, and then a stimulus was flashed in one of the four visual quadrants — upper left, upper right, lower left or lower right. The patient had to report whether the stimulus was a perfect circle or had convex and concave deformations.

For each quadrant, the degree of stimulus deformation was adjusted from trial-to-trial using a staircase procedure, which made the task harder if performance was low and easier if performance was high, in order to home in on the deformation level required to yield 80% correct performance. The threshold deformation level was five times higher in AR's affected (upper left) quadrant than in any of the unaffected quadrants, revealing a specific deficit in contour curvature perception, just as the monkey neurophysiological data would predict. This helps to confirm the functional homology between human and monkey V4, and emphasizes the role of V4 in curvature perception.

Similar results were obtained for the discrimination of curvature in spiral gratings and concentric 'Glass' patterns — random dot patterns in which pairs of dots are oriented along concentric circles. AR was also impaired, in the affected upper left quadrant, at discriminating the orientation of 'illusory' contours formed by borders between sinusoidal grating textures. Finally, AR appeared less able to judge the relative positions of object parts. The stimuli in this case were disks divided into a black half and a white half (Figure 2b). The amount of time required to determine which half was on top was approximately seven times greater in the affected quadrant. This is consistent with monkey neurophysiological data suggesting that area V4 encodes the relative positions of object parts [7]. In contrast to the results described so far, AR's ability to perform simple discriminations of luminance, grating orientation and motion direction appeared to be unaffected by the lesion. Thus, AR's deficits relate specifically to the kind of intermediate shape information thought to be processed by area V4.

Gallant *et al.* [1] also studied attention-related phenomena; example stimuli from one of the tests used are shown in Figure 2c. The task was to determine whether grating orientation was perfectly vertical or slightly oblique. AR's performance in all quadrants was normal when the grating was presented alone; the threshold for 80% correct performance was 5°. But when surrounding distractors were present, the threshold shot up to above 20° in the upper left quadrant (without changing in the other quadrants). Similar behavioral results have been demonstrated in

**Figure 2**




Stimuli used by Gallant *et al.* [1] and Wilkinson *et al.* [2] to study V4 function in humans. **(a)** Circle stimuli with varying degrees of deformation, used by Gallant *et al.* to test curvature perception. **(b)** Black and white disks used by Gallant *et al.* to study perception of object part location. **(c)** Stimuli used by Gallant *et al.* to test perception of grating orientation in the presence (left) or absence (right) of surrounding distractor stimuli. **(d)** Stimuli used by Wilkinson *et al.* to test human V4v activation by concentric (left), radial (middle) and linear (right) gratings.

monkeys with V4 lesions [13]. These lesion effects relate to neurophysiological studies showing strong modulation of V4 responses with selective attention [8]. V4 neural responses are suppressed by nearby distractors, but responses go back up if the monkey voluntarily attends to the stimulus [14]. Together, these findings argue that V4 is important, in both humans and monkeys, for focusing attention in complex scenes.

Wilkinson *et al.* [2] took a different experimental approach by measuring brain activity in normal human subjects using fMRI. They contrasted responses in three visual areas: V1 and V4 (both identified by topographical visual field mapping) and the fusiform face area (FFA), a region of human ventral temporal cortex thought to be specifically involved in face perception [15] (and identified here by its relatively selective activation by face stimuli). The stimulus set used was based on previous monkey neurophysiological studies which showed that V4 cells are generally more responsive to concentric and radial gratings than they are to linear gratings (Figure 2d) [5]. This response bias was seen with human V4 too: the activation levels produced by concentric and radial gratings were roughly equal to each other, and substantially higher than activation levels produced by linear gratings. This pattern was apparently unique to area V4; in area V1, there were no significant differences in activation by the three stimulus types. In the FFA, activation by concentric gratings was markedly higher than activation by other stimuli, perhaps reflecting FFA's supposed role in processing round objects (faces).

The unique correlation human V4 activation levels and single-cell responses in monkey V4 confirms the homology between the areas in the two species. The results also emphasize the role of V4 in intermediate shape processing. Wilkinson *et al.* [2] interpret their findings — and the prior neurophysiological data — as implying that V4 has a specialised role in the processing of concentric and radial patterns. As they note, however, the results are also consistent with general processing of curved and angled contours (compare with [6]), of the sort contained within the concentric and radial grating stimuli used in this experiment. The investigation by fMRI of human V4 using a greater variety of stimuli containing curves and angles would help to distinguish between these two interpretations.

Together, these two studies [1,2] greatly increase our confidence in the homology between the human and monkey visual areas that have been labelled V4. This makes physiological and anatomical investigations of detailed neural mechanisms in monkey V4 more clearly relevant for understanding human vision. These studies additionally provide important evidence concerning V4's role in intermediate shape processing and attentional filtering. The accelerating trend towards convergent human/monkey studies of this sort will greatly enrich our understanding of how we perceive and interpret the visual world.

## References


1. Gallant JL, Shoup RE, Mazer JA: **A human extrastriate area functionally homologous to macaque V4.** *Neuron* 2000, **27:**227-235.
2. Wilkinson F, James TW, Wilson HR, Gati JS, Menon RS, Goodale MA: **Radial and concentric gratings selectively activate human extrastriate form areas: an fMRI study.** *Curr Biol* 2000, **10:**1455-1458.
3. Ungerleider LG, Mishkin M: **Two cortical visual systems.** In *Analysis of Visual Behavior*. Edited by Ingle DG, Goodale MA, Mansfield RJQ. Cambridge, MA: MIT Press; 1982:549-586.
4. Zeki S: **Colour coding in rhesus monkey prestriate cortex.** *Brain Res* 1975, **53:**422-427.
5. Gallant JL, Connor CE, Rakshit S, Lewis JW, Van Essen DC: **Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey.** *J Neurophysiol* 1996, **76:**2718-2739.
6. Pasupathy A, Connor CE: **Responses to contour features in macaque area V4.** *J Neurophysiol* 1999, **82:**2490-2502.
7. Connor CE, Preddie DC, Gallant JL, Van Essen DC: **Spatial attention effects in macaque area V4.** *J Neurosci* 1997, **17:**3201-3214.
8. Moran J, Desimone R: **Selective attention gates visual processing in the extrastriate cortex.** *Science* 1985, **229:**782-784.
9. DeYoe EA, Carman GJ, Bandettini P, Glickman S, Wieser J, Cox R, Miller D, Neitz J: **Mapping striate and extrastriate visual areas in human cerebral cortex.** *Proc Natl Acad Sci USA* 1996, **93:**2382-2386.
10. Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RB: **Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging.** *Science* 1995, **268:**889-893.
11. Zeki S, Watson JD, Lueck CJ, Friston KJ, Kennard C, Frackowiak RS: **A direct demonstration of functional specialization in human visual cortex.** *J Neurosci* 1991, **11:**641-649.
12. Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RB: **Retinotopy and color sensitivity in human visual cortical area V8.** *Nat Neurosci* 1998, **1:**235-241.
13. De Weerd P, Peralta MR III, Desimone R, Ungerleider LG: **Loss of attentional stimulus selection after extrastriate cortical lesions in macaques.** *Nat Neurosci* 1999, **2:**753-758. [Published erratum appears in *Nat Neurosci* 2000 **4:**409].
14. Reynolds JH, Chelazzi L, Desimone R: **Competitive mechanisms subserve attention in macaque areas V2 and V4.** *J Neurosci* 1999, **19:**1736-1753.
15. Kanwisher N, McDermott J, Chun MM: **The fusiform face area: a module in human extrastriate cortex specialized for face perception.** *J Neurosci* 1997, **17:**4302-4311.